THE BEHAVIOURAL BASIS OF CRUSTACEAN DISTRIBUTION IN A TIDALLY MIXED ESTUARY

Net flow in estuaries is seawards, exposing swimming animals to the risk of export to the sea. This has led to numerous investigations of mechanisms facilitating estuarine retention (Naylor, 1988). Generalisations are difficult however, partly because of differences in estuarine circulation patterns. Also, different species may be more abundant in different parts of an estuary, implying that various behavioural mechanisms may be instrumental in maintaining observed distributions. The area studied was the Conwy Estuary, the largest in North Wales, which is almost completely mixed. Here, retention strategies based on laminar flow (Cronin and Forward, 1982) cannot operate. This work investigates behavioural retention strategies of species from various habitats within the estuary, and explores the relationship between behaviour, retention and distribution.

Probably the most significant behavioural strategy is that of the planktonic copepod *Eurytemora affinis*, a euryhaline species, most numerous in the low salinity zone. Drift-net sampling on rising spring tides showed copepod abundances in the water column to be concentrated on flood tides at downstream sites and on the ebb tide at the most upstream site. This suggests a preferred region in which the majority of animals are found. Sampling over each tidal cycle for two weeks at a mid-estuary site showed distinct semi-lunar variation of the tidal abundances of *E. affinis*. Greatest abundance over neap tides was on the ebb, but was on flood tides over springs, suggesting that the population maximum moved upstream on springs and downstream on neaps. To test this, plankton samples were taken on three separate spring and neap tides. Each time a distinct population maximum was found, the position of which was further seaward on neap than on spring tides.

Independent oceanographic studies on the Conwy estuary (Shiono and West, 1987) suggest no physical mechanism which could explain these observations on the basis that *E. affinis* behaves as a passive particle. Extensive horizontal swimming by animals of this size seemed equally unlikely, but vertical migrations into the water column at different times was an attractive working hypothesis

Endogenous locomotor activity was therefore tested for as a possible behavioural basis to these observations. Swimming activity was measured under constant conditions in the laboratory using an infra-red light beam actograph and a free-running activity rhythm in phase with the time of expected high tide was found, apparently the first in a copepod. This suggests that *E. affinis* moves into its preferred salinity zone by swimming, under endogenous control, on the state of tide providing transport in the appropriate direction. The position of this zone varies with the semi-lunar cycle, and the swimming activity of the animals appears to change accordingly.

Different retention strategies are adopted by two species of amphipod, *Gammarus zaddachi* and *Corophium volutator*. Both swim periodically in the water column and so risk export from the estuary. *C. volutator* was found fairly consistently at the mid-estuary locations, but *G. zaddachi* varied its position throughout the year with respect to salinity as also reported elsewhere by Girish *et al*, (1975). Overwintering adults and developing juveniles occurred high up the estuary whereas reproducing adults were most common in mid-estuary. Thus the adult population, particularly ovigerous females, move downstream while juveniles migrate upstream. Significantly no *G. zaddachi* were recorded at the most seaward site.

Experimental studies demonstrated the presence of endogenous swimming rhythms in both amphipod species, but that each exhibited different kinetic swimming responses in a flume tank. *G.zaddachi* showed increased swimming in higher current velocities, whereas *C. volutator* showed the opposite response. Thus *G. zaddachi* appears to use a combination of endogenously timed swimming behaviour and responsiveness to water flow to vary its position along the estuary, while *C. volutator* appears to avoid moving water and so limits displacement from its preferred habitat.

In conclusion several strategies appear to have evolved by which estuarine crustacean species maintain their distributions in an environment of net flow seawards. Moreover, the precise nature of the zonations found in each species suggest that in the Conwy Estuary, behaviour is finely tuned to ensure retention in specific environments within the estuary and not simply within the estuary itself.

Acknowledgements

The authors wish to thank the Natural Environment Research Council (U.K.) for travel and studentship funding for ARH.

Literature Cited

Cronin, T.W. and Forward, R.B. Jr. 1982. Tidally timed behaviour: Effects on larval distributions in estuaries. In V.S. Kennedy (ed) 'Estuarine comparisons'. (Academic Press: New York).

Girish, H.B., Dieleman, J.C. Petersen, G.W. and Pinkster, S. 1974. The migration of two sympatric gammarid species in a French estuary. Bijdragen tot de Dierkunde **44**: 239-273.

Naylor, E. 1988. Rhythmic behaviour of decapod Crustacea. Symposium of the Zoological Society of London **59**: 177-199.

Shiono, K. and West, J.R. 1987. Turbulent perturbations of velocity in the Conwy Estuary. Estuarine, Coastal and Shelf Science **25**: 533-553.

Andrew R. Hough and Ernest Naylor, School of Ocean Sciences, University College of North Wales, Menai Bridge, Wales LL59, UK.